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THE TAXONOMY OF VERNONIA ACAULIS, V. GLAUCA AND V. NOVEBORACENSIS (COMPOSITAE)

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Delimitation and identification of all taxonomic units are extremely difficult in the genus *Vernonia* since there are numerous, intermediate, perplexing forms (Ekman, 1914). One postulation is that the genus underwent rapid evolution in North America following the Cretaceous Period and that it is probably still evolving (Jones, 1964). This has resulted in the formation of population systems that appear somewhat morphologically disinct yet taxonomically difficult. Because the reproductive barriers among many of the species are incomplete (Jones, 1966, 1967), and because hybridization occurs commonly where species show biotic or adjacent sympatry, the genus is of interest from both evolutionary and taxonomic viewpoints.

The three species *Vernonia acaulis* (Walt.) Gleason, *V. glauca* (L.) Willd. and *V. noveboracensis* (L.) Michx. are the most eastern in the United States. They occur from Massachusetts to eastern Kentucky and Tennessee, and into Florida and Alabama along the Coastal Plain, Piedmont and mountains. The number of synonyms for the latter two species is an indication of the uncertainty which has characterized their treatment during the past 200 years. It is also obvious that the ranges of the three species have been poorly understood. The reason for this is that their

ranges were often copied from earlier floras which were erroneous. These taxa were chosen for systematic study because of the conspicuous variability within the taxa, especially in *V. noveboracensis*. The usual field and herbarium studies were supplemented by biosystematic investigations.
In the course of this investigation, assistance has been received from many persons. It is not possible to thank them all specifically, but my sincere thanks are none the less real. This work was supported by National Science Foundation grant GB 7208 and the University of Georgia. Specimens for examination were obtained from the following herbaria: ALU; AUA; FSU; FLAS; GA; GH; NCU; NY; OS; PH; SMU; US; TENN; VDB; WIS; WVA. Annotated specimens of the three taxa may be found in all of these herbaria.

HISTORICAL ACCOUNT

Walter (1788) applied the name *Chrysocoma acaulis*, and he was clearly referring to a plant with a basal cluster of leaves. Michaux (1803) described the same taxon and gave it the name *Vernonia oligophylla*. In 1891 Kuntze applied the generic name of *Cacalia*. In 1906 Gleason recognized the name of Walter and made the combination *Vernonia acaulis* (Walt.) Gleason. *Vernonia georgiana* Bartlett has been shown to be a hybrid between *V. acaulis* and *V. angustifolia* Michx. (Jones, 1967).

It is obvious from an examination of the microfiche of the Linnaean Herbarium that Linnaeus' (1753) *Serratula noveboracensis* refers to *Vernonia noveboracensis*. Apparently his *Serratula praealta* differed from the type only in the shorter appendages of the involucral bracts (Gleason, 1906). Walter's (1788) *Chrysocoma tomentosa* shows no essential difference from *V. noveboracensis*. Michaux (1803) transferred the species to the genus *Vernonia* making the combination *V. noveboracensis* (L.) Michx. He also recognized *V. praealta*. Hill (1768) applied the generic name *Behen*, and Miller in 1768 used the name *Serratula caroliniana* Mill. Walter's (1788) *Chrysocoma tomentosa* was recognized by Elliott (1824); however, Elliott was not certain that his

plant was the same as that described by Walter. More recently, Steele (1901) discussed the matter, and regarded the name *V. tomentosa* Ell. to be a plant of wet places from the south Atlantic Coast. Gleason (1906) studied Steele's specimens and felt that they did not warrant its separation as a distinct species. According to Gray (1852), *V. rugeliana* Shuttlew. is the ordinary form of *V. noveboracensis*. The next major addition to the synonomy was that of *V. harperi* Gleason (1906). It is based on *Harper* 1424 from Coffee County, Georgia. Gleason distinguished it from *V. noveboracensis* because of its larger heads and more numerous flowers.

Serratula glauca L. was based on a plant collected by Clayton, studied by Linnaeus and fragments were given to Asa Gray in 1839 (Fernald, 1941). Willdenow (1804) made the combination *Vernonia glauca* (L.) Willd. Gray (1884) included *V. glauca* as part of *V. noveboracensis* var. *latifolia*. Britton's (1898) description of *V. noveboracensis tomentosa* (Walt.) Britton refers to *V. glauca*. In 1941 Fernald described *V. glauca* (L.) Willd. forma *longiaristata* Fernald which has longer bract tips.

SYSTEMATIC TREATMENT

Key to Species

1. Principal leaves basal, the stem leaves usually much reduced ..... 1. *V. acaulis*
1. Principal leaves cauline, the stem leaves usually not reduced except near inflorescence 2
   2. Pappus straw-colored to white, lower surface of leaves paler than upper; leaves usually rather abruptly narrowed at base; plants of well drained soil; normally flowering in July ..... 2. *V. glauca*
   2. Pappus purple or brownish-purple, lower surface of leaves not much paler than upper; leaves gradually narrowed at base; plants of moist soil; normally flowering in August and September ..... 3. *V. noveboracensis*

1. *Veronia acaulis* (Walt.) Gleason, Bull. N.Y. Bot. Gard. 4: 222. 1906.
   Chrysocoma acaulis Walt., Fl. Car. 196. 1788.
   Type: Not examined. Photograph of type in PH.

Vernonia oligophylla Michx., Fl. Bor.-Am. 2: 94. 1803.
Cacalia acaulis Kuntze, Rev. Gen. 968. 1891.

Stems erect, glabrous to thinly puberulent, simple to the inflorescence, 3-10 dm high. Leaves mostly basal, basal leaves 20 (12-30) cm long, 7 (4-10) cm wide, oblong to obovate, sparsely pubescent above, sparsely pubescent to nearly glabrous below, tip acute, base attenuate, margins coarsely and irrgularly serrate, cauline leaves bractlike. Inflorescence loose and open branched. Heads 42 (31-59) flowered. Involucre broadly campanulate, 6.6 (5.0-8.5) mm high, 7.0 (5.7-8.5) mm wide. Bracts lanceolate to linear elliptic. Bract tips acuminate to long acuminate. Bracts greenish-purple, thinly puberulent on back. Achenes sparsely pubescent, strongly ribbed, resinous, 3 (2.7-3.2) mm long. Pappus straw colored to white, bristles 5.5-9.0 mm long, scales narrow, 0.5-1.0 mm long. Flowering in July. Chromosome number $n = 17$. Habitat: uplands, sandy woods, flat-

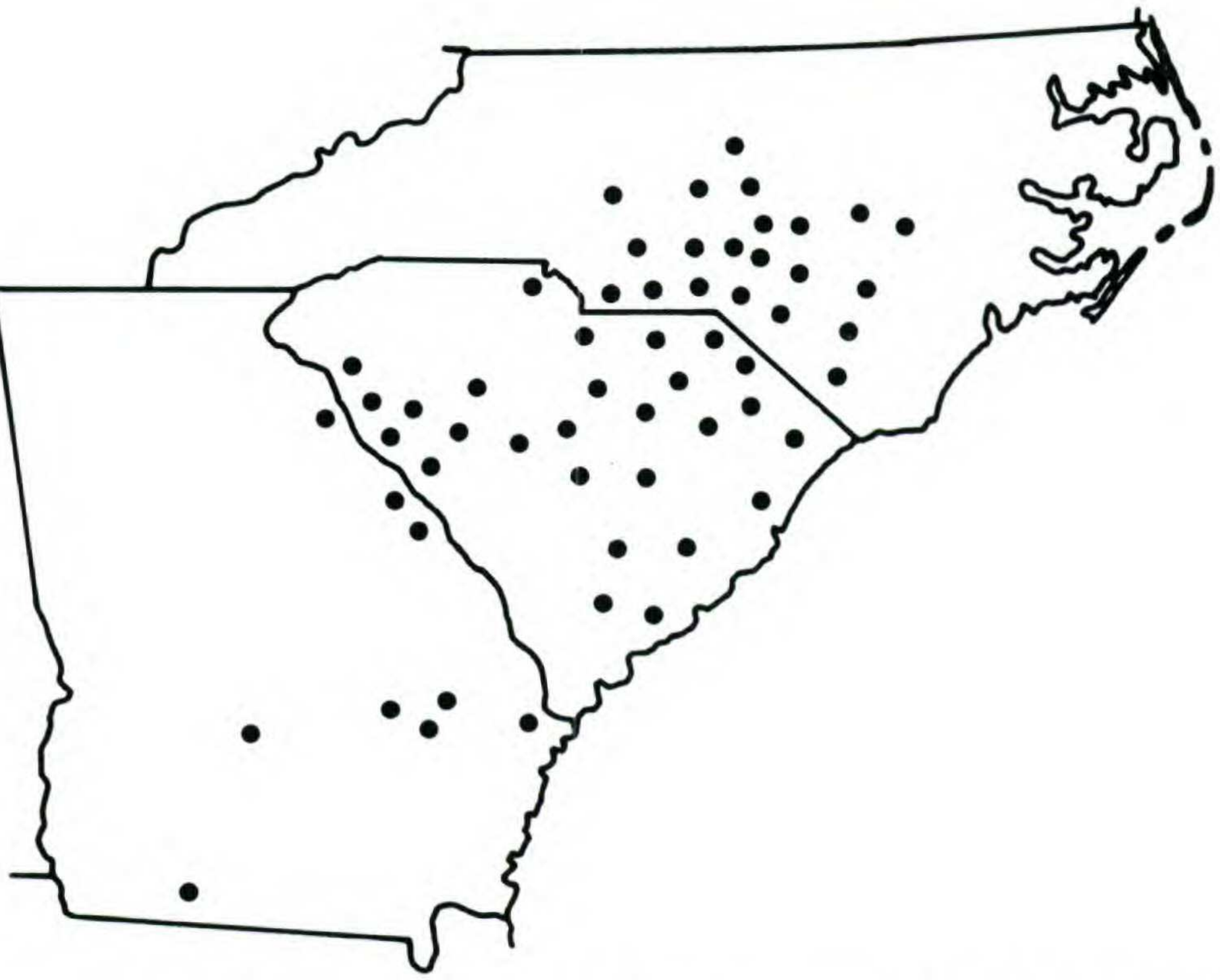

Figure 1. Distribution map of *Vernonia acaulis* based on county distributions.

woods and sandhill ecotones. Distribution: in part of Coastal Plain and Piedmont of North Carolina, South Carolina, Georgia (see Fig. 1).

Vernonia acaulis is quite distinct and is easily identified. Occasionally, it does hybridize with *V. noveboracensis* and *V. angustifolia* Michx. The F_1 hybrids are easy to recognize as they are intermediate between their parents. This hybridization does not seem to have blurred the species lines. Local population samples were made in Elbert Co., Ga. (15736) and Montgomery Co., N. C. (15783). Transplants were grown in the garden and the greenhouse from these two locations. Table 1 presents the sample means, standard deviations, coefficients of variation and ranges of certain morphological characters from the North Carolina population. There is probably no more variation between local populations than one would normally expect in outbreeding population systems. Experimental hybrids were made among *V. acaulis*, *V. noveboracensis*, *V. glauca* and *V. angustifolia*. The F_1 hybrids were intermediate. They had good pollen stainability with aniline blue in lactophenol and good pairing of the chromosomes at meiosis.

TABLE 1

Vernonia acaulis: population sample means ($\bar{x}$), standard deviations (s), coefficients of variation (C) and ranges of seven morphological characters; n = 25; population sample 15783, Montgomery Co., N. C.

Character	$\bar{x}$	s	C	Range
lower leaf width cm	6.5	1.4	0.2	3.7 - 10.0
lower leaf length cm	20.2	4.0	0.2	12 - 30
middle leaf width cm	0.7	0.4	0.6	0.2 - 2.0
middle leaf length cm	8.7	3.9	0.4	1.7 - 15.6
involucre width mm	7.0	0.7	0.1	5.7 - 8.5
involucre length mm	6.6	0.9	0.1	5.0 - 8.5
flowers per head	41.8	7.0	0.2	31 - 59

Normally, *Vernonia acaulis* is ecologically isolated from *V. angustifolia*. The latter usually grows in drier places than the former. It is also ecologically as well as seasonally isolated from *V. noveboracensis*. *Vernonia acaulis* flowers in July, while *V. noveboracensis* flowers in August. The habitat in which *V. noveboracensis* grows is often quite wet, while *V. acaulis* grows in well-drained soil. Isolation, however, is not always completely effective as the flowering periods may overlap or the ecological niches may be within a few meters of each other.

2. *Vernonia glauca* (L.) Willd., Sp. Pl. 3: 1633. 1804.
Serratula glauca L., Sp. Pl. 818. 1753.
Type: According to Fernald (1941), it is based on a specimen collected by Clayton, studied by Linnaeus and fragments given to Gray in 1839. Not examined.
Suprago glauca Gaertn., Fruct. 2: 402. 1791.
Vernonia noveboracensis latifolia A. Gray, Syn. Fl. N. Am. **1:** 89, in part. 1884.
Vernonia noveboracensis tomentosa Britton, Britt. & Brown. Ill. Fl. 3: 302, in part. 1884.
Vernonia glauca (L.) Willd. forma *longiaristata* Fern., Rhodora **43:** 652. 1941.

Stems erect, glabrous, simple, 10-16 dm high. Leaves numerous, 15 (12.5-19) cm long, 5 (3.4-7.4) cm wide, ovate-lanceolate to almost ovate, glabrous or scabrellate above, pale and thinly puberulent below, tips short-acuminate, abruptly narrowed at the base, margins irregularly dentate to nearly entire. Inflorescence compact. Heads 40 (32-48) flowered. Involucre broadly campanulate 7.3 (5.0-8.8) mm high, 7.4 (6.1-8.5) mm wide. Bracts, inner lance-ovate, outer lanceolate, bract tips acute or acuminate to long acuminate. Bracts greenish-purple, glabrous or puberulent. Achenes nearly glabrous, ribbed, 3 (2.7-3.3) mm long. Pappus straw-colored to white, bristles 6.7 mm long, scales narrow 0.4-0.8 mm long. Flowering in July. Chromosome number, $n = 17$. Habitat: edge of well-drained upland oak-hickory woods. Distribution: mountains and piedmont from Pennsylvania to Alabama (see Fig. 2).

Figure 2. Distribution map of *Vernonia glauca* based on county distributions.

Local population samples were collected in Clarke Co., Ga. (15146) and in Orange Co., N. C. (15788). Transplants were grown in the greenhouse and garden from the above locations and also from Gwinnett Co., Ga. (15349). Experimental hybrids were produced with a number of other species of *Vernonia*, including *V. noveboracensis* and *V. acaulis*. The F_1 hybrids had good chromosome pairing at meiosis, and the pollen stained well with aniline blue in lactophenol.

Although misinterpretation of *Vernonia glauca* versus *V.*

noveboracensis is common, *V. glauca* is morphologically and ecologically distinct from the latter. There is some variation within and between the populations; however, this variation is probably no more than is normally expected in heterozygous individuals and populations. This normal variation includes Fernald's (1941) forma *longiaristata*, and it is certainly not worthy of a name. Table 2 presents some morphological measurements from one sample.

TABLE 2

Vernonia glauca: population sample means ($\bar{x}$), standard deviations (s), coefficients of variation (C) and ranges of six morphological characters; n = 25; population sample 15146 Clarke Co., Ga.

Character	$\bar{x}$	s	C	Range
middle leaf width cm	4.9	1.0	0.2	3.4 - 7.4
middle leaf length cm	15.7	1.7	0.1	12.5 - 19.0
involucre width mm	7.4	0.6	0.1	6.1 - 8.5
involucre length mm	7.3	0.9	0.1	5.0 - 8.8
flowers per head	40.5	4.4	0.1	32 - 48
ratio middle leaf length/width	3.3	0.6	0.2	2.4 - 5.0

Natural hybrids between *Vernonia glauca* and *V. flaccidifolia* Small were collected in Gwinnett Co., Ga. (15349). The parents and the hybrids were at the edge of oak-hickory woods and in flower at the same time. During the course of this study no specimens of natural hybrids between *V. glauca* and *V. noveboracensis* were unequivocally designated. They should, however, be looked for. These two species are normally seasonally and ecologically isolated. *Vernonia glauca* flowers in July, while *V. noveboracensis* blooms in August. In addition, the former grows in well-drained upland woods and is rarely found in the lowlands, while the latter is found in wet meadows, low roadsides, and stream banks and found often in standing water. Experimental F_1 hybrids are intermediate between their parents in the key characters of pappus color and leaf shape.

Figure 3. Distribution map of *Vernonia noveboracensis* based on county distributions.

3. *Vernonia noveboracensis* (L.) Michx. Fl. Bor.-Am. 2: 95. 1803.

Serratula noveboracensis L., Sp. Pl. 818. 1753.

Type: Not examined, photograph of type in microfiche of Linnaean Herbarium. Photograph of type in GH.

Serratula praealta L., Sp. Pl. 818. 1753.

Behen noveboracensis Hill, Hort. Kew. 68. 1768.
Behen praealtum Hill, Hort. Kew. 68. 1768.
Serratula caroliniana Mill., Gard. Dict. ed. 8. Serratula no. 7, 1768.
Chrysocoma tomentosa Walt., Fl. Car. 196. 1788.
Vernonia praealta Michx., Fl. Bor.-Am. **2**: 95. 1803.
Vernonia tomentosa Ell., Bot. S. C. & Ga. **2**: 288. 1821.
Vernonia noveboracensis (L.) Michx. var. *praealta* Wood, Classbook 183. 1845.
Vernonia rugeliana Shuttlew.; A. Gray, Pl. Wright. **1**: 82. 1852.
Vernonia noveboracensis (L.) Michx. var. *latifolia* A. Gray, Sym. Fl. N. Am. **2**: 89. 1884.
Cacalia noveboracensis Kuntze, Rev. Gen. 324. 1891.
Vernonia noveboracensis tomentosa Britton, Porter & Britton, Mem. Torrey Bot. Club **5**: 311. 1894.
Vernonia harperi Gleason, Bull. N. Y. Bot. Gard. **4**: 221. 1906.

Stems erect, glabrous to thinly pubescent, simple to the inflorescence 10-25 dm high. Leaves numerous, 18 (12-28) cm long, 3.4 (1.3-5.5) cm wide, lanceolate, glabrous or scabrellate above, thinly tomentose below, tip acuminate, base attenuate, margins nearly entire. Inflorescence loose and spreading. Heads 44 (30-65) flowered. Involucre campanulate, 12 (7-17) mm high, 7.7 (6-10) mm wide. Bracts triangular-ovate. Bract tips acuminate to long acuminate with a filiform appendage. Bracts greenish-purple, pubescent and sometimes ciliate. Achenes sparsely pubescent, ribbed, 4.1 (4-4.5) mm long. Pappus brownish-purple, bristles 6.5 (6-7) mm long, scales linear, 0.4-0.8 mm long. Corollas whitish and pappus pale in forma *albiflora* Britton, 1890, Bull. Torrey Bot. Club 17: 124. Corollas lilac in forma *lilacina* Oswald, 1957, Phytologia 5: 465. Flowering in August and September. Chromosome number, $n = 17$.
Habitat: low, wet roadsides, wet meadows, creek banks.
Distribution: piedmont, coastal plain and mountains from Massachusetts to eastern Kentucky and eastern Tennessee into Alabama and Florida (see Fig. 3).

Of the three taxa, *Vernonia noveboracensis* is by far the most variable, and it has the greatest geographical range. In Gleason's (1906) revision of *Vernonia*, the species group *Noveboracenses* included two species *V. noveboracensis* (L.) Willd. and *V. harperi* Gleason. The former has a wide distribution from Alabama to Massachusetts on the Atlantic Coastal Plain, Piedmont Plateau, and the mountains. According to Gleason (1923), it gave rise to *V. harperi* of the Atlantic Coastal Plain in south Georgia; this species has larger heads with more flowers. As Ekman (1914) noted, however, Gleason's species are very small, narrowly defined and, as a rule, based upon very meager material.

The purpose of this phase of the study was to investigate the biological complexity of *Vernonia noveboracensis* and *V. harperi* in order to help clarify their systematics. In this study observations and conclusions were based on field work, on analysis of local population samples, on garden studies, on laboratory work, and on examination of herbarium specimens.

Population samples: Local population samples (mass collections) of 25 individuals each were made from four localities in Georgia in late August and September of 1967. These provided a transect from the mountains to the Coastal Plain. Population sample 15048 was collected in a wet pasture in White County in the Blue Ridge Mountains and is designated as BR. Population sample 15117 was made from a colony growing on a low moist roadside in Greene County in the Piedmont Plateau and is called PP. A wet pasture in McDuffie County near the Fall Line provided 15144, and it is labeled FL. Population sample 15086 was collected from a wet power line right-of-way in Tattnal County, just a few miles from the type location of *V. harperi*. Tattnal County is in the Atlantic Coastal Plain, and this sample is designated as AC. Characters in which *V. harperi* and *V. noveboracensis* differ, as well as characters in which they are similar, were used in scoring the specimens. Ten characters were measured or scored on each individual from the samples. The numerical values thus ob-

tained were then punched on IBM cards. The characters were as follows: (1) width of the middle stem leaves (cm); (2) length of the middle stem leaves (cm); (3) pubescence of the middle stem leaves (for scoring purposes, categories were set up from 1 = glabrous to 6 = pubescent with hairs over .25 mm long and crowded); (4) dots on lower leaf surface range from 1 = not dotted to 3 = strongly dotted; (5) bract tip shape (9 categories were established for scoring purposes; however, these populations were all scored either 8 or 9); (6) pappus color, range from 1-5, with 1 = off-white to 5 = brown with a purple tinge; (7) involucre width (mm); (8) involucre length (mm); (9) number of flowers per head; (10) leaf length/width ratio.

The population samples were compared using the computer program BMDO7M, Stepwise Discriminant Analysis, version of 1 Sept. 1965, Health Sciences Computing Facility, UCLA. The program is a type of multi-variant analysis using a stepwise fitting in which the sums of squares and products are re-arranged at each stage of the fitting so that the variable giving the largest reduction of the residuals is the next one fitted. The standard deviations and means were obtained from the print-out of this program. From these the coefficients of the variation were determined. The variable characters within and between the populations were compared using scatter diagrams and polygons.

The type specimen of *Vernonia harperi* was similar to

TABLE 3

Number of cases of *Vernonia noveboracensis* classified into group by BMDO7M, Stepwise Discriminant Analysis Program.

Population[1]	BR	PP	FL	AC
BR	15	6	4	0
PP	0	25	0	0
FL	2	0	22	1
AC	0	0	0	25

[1]Blue Ridge (BR); Piedmont Plateau (PP); Fall Line (FL); Atlantic Coastal Plain (AC).

certain of the AC plants. Analysis of herbarium specimens indicated that there is variation in *V. noveboracensis*; however, the changes in characters are either gradual over long distances or not correlated geographically or morphologically with other characters. The results from the computer transect analysis indicated that all populations were somewhat distinct (see Table 3). However, PP and AC individuals would not have been misclassified into the other three populations. On the other hand, some BR plants would have been classified into PP and FL. Likewise, FL had some plants which fell into BR and AC.

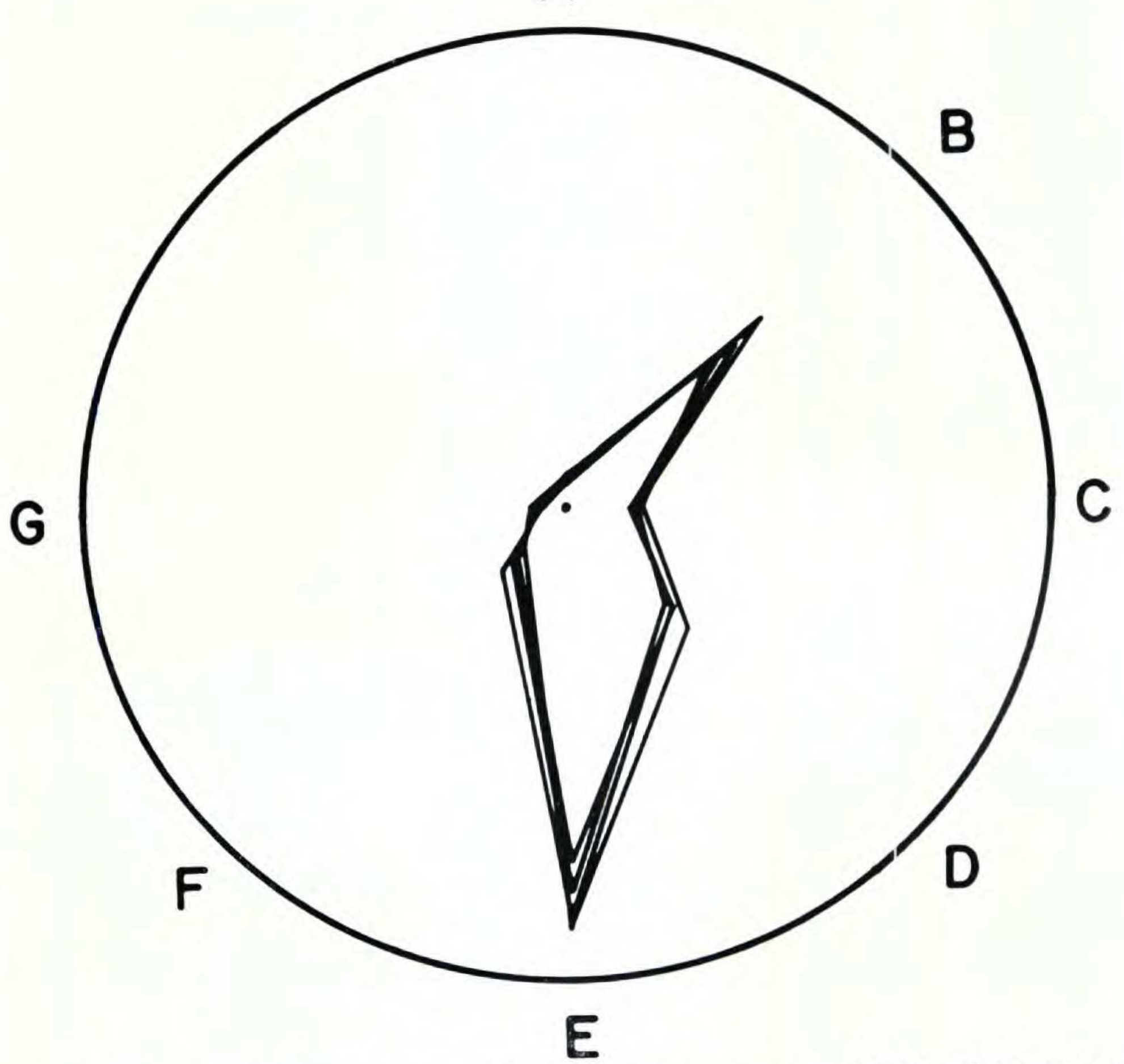

Figure 4. Polygons based on the sample means of the four populations (BR, PP, FL, AC) of *Vernonia noveboracensis*. A, leaf width; B, leaf length; C, involucre width; D, involucre length; E, number of flowers per head; F, ratio of leaf length/width; G, pubescence score.

On the basis of the multi-variant analysis, the value of the characters presented in Table 4, the coincidence of the polygons (Fig. 4) and the scatter diagram (Fig. 5), some differentiation is indicated, yet the populations are probably indistinguishable. Grant (1963) has indicated that most outbreeding populations are variable or polymorphic. He noted that this is due to the diversity in the allelic forms of one or more genes. Since allelic forms do exist, no single

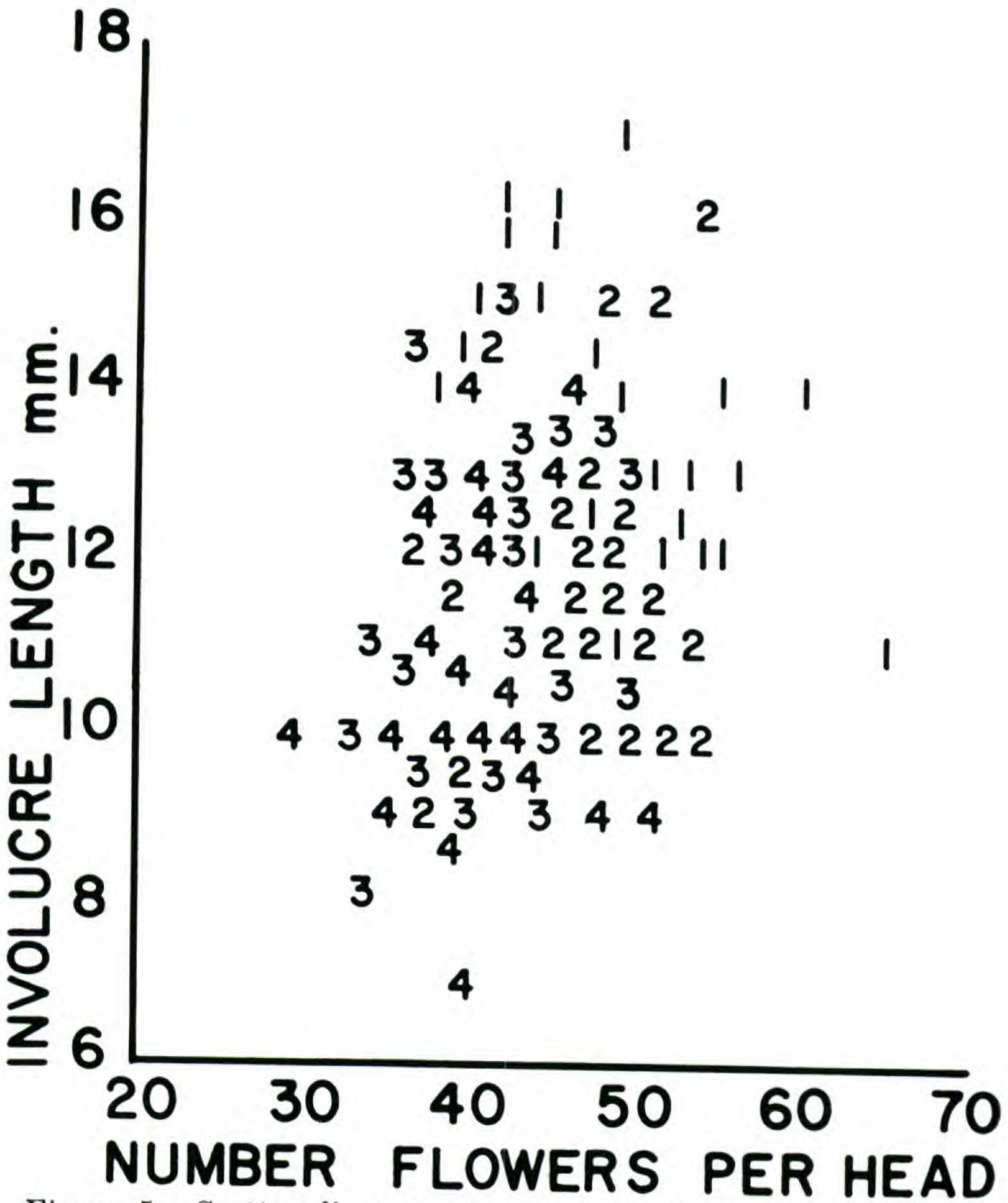

Figure 5. Scatter diagram of individuals of the four populations (AC, 1; FL, 2; PP, 3; BR, 4) of *Vernonia noveboracensis*.

individual will carry all the genetic variation found within the populations. The breeding population maintains and stores this genetic variation which is conserved by the reproductive process. Changes in the allelic frequencies could be caused by mutation, gene flow, natural selection and genetic drift.

Chromatographic patterns: The chromatographic patterns of the phenolic compounds of eight individuals from each population sample (BR, PP, FL and AC) were investigated through the use of 2-dimensional paper chromatography. Dried flower heads were extracted in 1% HCl in methanol for 30 hours, and the extracts were concentrated by evaporation. About 1 ml of the extract was applied in one spot to Whatman 3 MM chromatographic paper and then developed by the descending method. Development employed the following solvents in the order listed: (1) tertiary butanol:acetic acid:water (3:1:1 v/v for 24 hours), and (2) acetic acid:water (15:85 v/v for four hours). Upon drying the chromatograms were examined in daylight, in transmitted longwave ultra-violet light (UV) both with and without the presence of ammonia vapor, and by reflected UV light after having been sprayed with Benedict's solution. Each plant was chromatographed twice.

Twenty-two compounds were followed in the course of this study. No attempt was made to identify the compounds; however, color reactions with several reagents indicated that most were probably phenolic compounds. Although some compounds were either absent or below the threshold of detection in certain of the plants from each population, no pattern was found that would serve to differentiate the populations.

Hybridization and garden experiments: Crosses were made in all possible combinations between BR, PP, FL, AC and between *Vernonia acaulis* and *V. glauca*. The F_1 hybrids were grown to maturity and pairing of the chromosomes was observed at meiosis. Pollen grains were stained in aniline blue in lactophenol for 24 hours. Transplants from several locations were observed in the garden and green-

TABLE 4

Vernonia noveboracensis: population sample means ($\bar{x}$), standard deviations (s), ranges, and coefficients of variation (C) of seven morphological characters that were variable within and between the populations.

Population[1]	$\bar{x}$	s	C	Range
Middle leaf width cm				
BR	3.8	0.8	0.2	2.4 - 5.5
PP	3.3	0.6	0.2	2.5 - 4.5
FL	2.5	0.7	0.3	1.3 - 4.3
AC	3.8	1.0	0.3	2.6 - 5.5
Middle leaf length cm				
BR	19.1	3.7	0.2	12.1 - 24.8
PP	21.8	3.8	0.2	14.5 - 28.0
FL	17.1	2.8	0.2	12.9 - 24.5
AC	16.5	2.6	0.2	12.4 - 21.0
Involucre width mm				
BR	7.0	0.7	0.1	6.0 - 8.5
PP	7.7	0.8	0.1	6.5 - 9.0
FL	7.3	0.8	0.1	6.0 - 9.2
AC	8.7	0.8	0.1	7.5 - 10.0
Involucre length mm				
BR	11.7	1.9	0.2	8.0 - 15.0
PP	10.7	1.8	0.2	7.0 - 14.0
FL	11.7	1.9	0.2	9.0 - 16.0
AC	13.8	1.8	0.1	11.0 - 17.0
Number of flowers per head				
BR	40.6	4.4	0.1	33 - 48
PP	40.4	4.4	0.1	30 - 49
FL	46.2	4.5	0.1	38 - 54
AC	48.9	6.6	0.1	39 - 65
Ratio leaf length/width				
BR	5.1	1.3	0.3	3.0 - 9.3
PP	6.6	1.1	0.2	3.7 - 8.8
FL	7.0	1.5	0.2	3.4 - 9.9
AC	4.6	1.2	0.3	2.6 - 7.3

Pubescence score				
BR	2.6	0.8	0.3	1 - 4
PP	2.8	0.4	0.2	2 - 3
FL	3.0	0.5	0.2	2 - 4
AC	3.3	0.6	0.2	2 - 4

[1]Blue Ridge (BR); Piedmont Plateau (PP); Fall Line (FL); Atlantic Coastal Plain (AC).

house for over two years. The F_1 hybrids were vigorous and had good chromosome pairing at meiosis. Pollen stainability was usually above 90%. All populations studied have a chromosome number of $n = 17$. The morphological variations seemed to be maintained in the transplant garden. Certain F_2 hybrids from the cross *V. noveboracensis* × *V. glauca* had reduced pollen stainability and poor chromosome pairing at meiosis. This indicates that hybrid breakdown may occur in later generations even though the F_1's are fertile.

Vernonia noveboracensis hybridizes with *V. altissima* Nutt. in eastern Tennessee, in eastern Kentucky and in Pennsylvania. This produces some specimens with smaller heads. In North Carolina *V. noveboracensis* hybridizes with *V. acaulis*. Also in that state, it may occasionally hybridize with *V. angustifolia* Michx. Herbarium specimens were observed that might possibly have been natural hybrids between *V. noveboracensis* and *V. glauca*. All of these hybrid combinations have been produced in the greenhouse. *Vernonia noveboracensis* is usually seasonally and ecologically isolated from *V. acaulis* and *V. glauca* where they are sympatric. The former blooms in August and September, while the latter two species flower in July. Also *V. noveboracensis* grows in much wetter soil than the other two. From an evolutionary viewpoint, the most important natural hybridization is that with *V. altissima* as some local introgression seems to have occurred.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

The presence of relatively few morphological and physiological differences is evidence of close relationships among

these three taxa. Gleason (1923) suggests that they may have been derived from the more primitive *Vernonia angustifolia* or, more likely, a common ancestor of all of our present day eastern species. Present evidence indicates that this was a logical assumption. The taxa considered here apparently diverged from a common ancestor during past geological history.

The species considered in this paper have several features in common, including around 40 flowers per head. In addition, they all have acuminate bract tips, although the tips of *Vernonia noveboracensis* are often filiform and longer. The pappus of both *V. glauca* and *V. acaulis* is straw-colored to white, whereas it is brown to purple in *V. noveboracensis*. The latter flowers in August while the other two species bloom in July. These characteristics are normally key characters in the species of *Vernonia* of eastern North America.

The basal leaves of *Vernonia acaulis* seem to function in reducing the competition from the sparse surrounding vegetation of its habitat. The cauline leaves and longer stems of the other two taxa seem to be of selective advantage in overcoming their competition, for they are generally taller than the plants around them. This is especially true with *V. noveboracensis* which grows in moist areas with vigorous competing vegetation. All three species begin to grow early in the spring.

Vernonia acaulis grows in uplands, sandy woods, well-drained flatwoods, and sandhill ecotones. Low, wet roadsides, wet meadows, and creek banks provide habitats for *V. noveboracensis*, whereas *V. glauca* is always found in well-drained, upland, oak-hickory woods.

Geographical isolation of segments of the ancestral population system, in conjunction with natural selection in response to influences of past changes in the earth's surface, climate and vegetation, could have produced the physiological and morphological differentiation of these species. Presently, the population systems appear to be separated

by prezygotic seasonal and ecological isolating mechanisms and by a postzygotic hybrid breakdown in F_2 generations.

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